ORGANS OF POSSIBLE STRIDULATORY FUNCTION IN WATER-BEETLES (COLEOPTERA: DYTISCIDAE)

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Abstract

Organs of possible stridulatory function are described from the genera *Laccophilus, Agabus, Carrhydrus, Colymbetes, Cybister,* and *Hydaticus.* Five major types of organs are recognized on the basis of the portions of the body on which they are found: file on submentum, plectrum on labial palpus; file on metacoxa, plectrum on metafemur; file on abdominal sterna, plectrum on metafemur; file on metafemur, plectrum on abdominal sterna; and file on protarsal article 2, plectrum on protibia. With a few exceptions these organs are restricted to, or best developed on, males.

Introduction

During the course of a taxonomic study of the Dytiscidae, Larson noted several examples of modifications of opposing body parts in which a roughened area or file on one matched with a projection on the other. Further search revealed that such structures were widespread in the family and that in each case one part could be moved over the other in a very precise manner. We wish to draw attention to this variety of interesting structures and to suggest a function for them. More than 200 species of Dytiscidae, representing nearly all the North American genera, have been examined, and we describe the major types of structure found. No attempt has been made to elucidate intraspecific variation, important as such variation may be.

Some of these structures have been described before as will be noted below, and some have been called "stridulatory organs" (e.g., Balfour-Browne 1940), although no behavioral observations are available. Almost all sounds that have been heard from dytiscid beetles have occurred when the animals were out of water and generally under some stress. Under these circumstances, attention has been focused on the wings as the means by which sound is produced (von Reeker 1891; Arrow 1924; Marcu 1936). However, we believe that such sounds could be produced simply by whirring the wings beneath the elytra. In particular, it seems unnecessary to invoke a stridulatory function for the 'costal file' as was done by von Reeker (1891), and more recently by Freitag and Lee (1972) to account for buzzing sounds made by cicindelid beetles. Indeed, all Adephaga that we examined had very similar costal architecture. We intend, therefore, to describe only those structures in the Dytiscidae that fit the conventional form of a specialized frictional stridulatory organ.

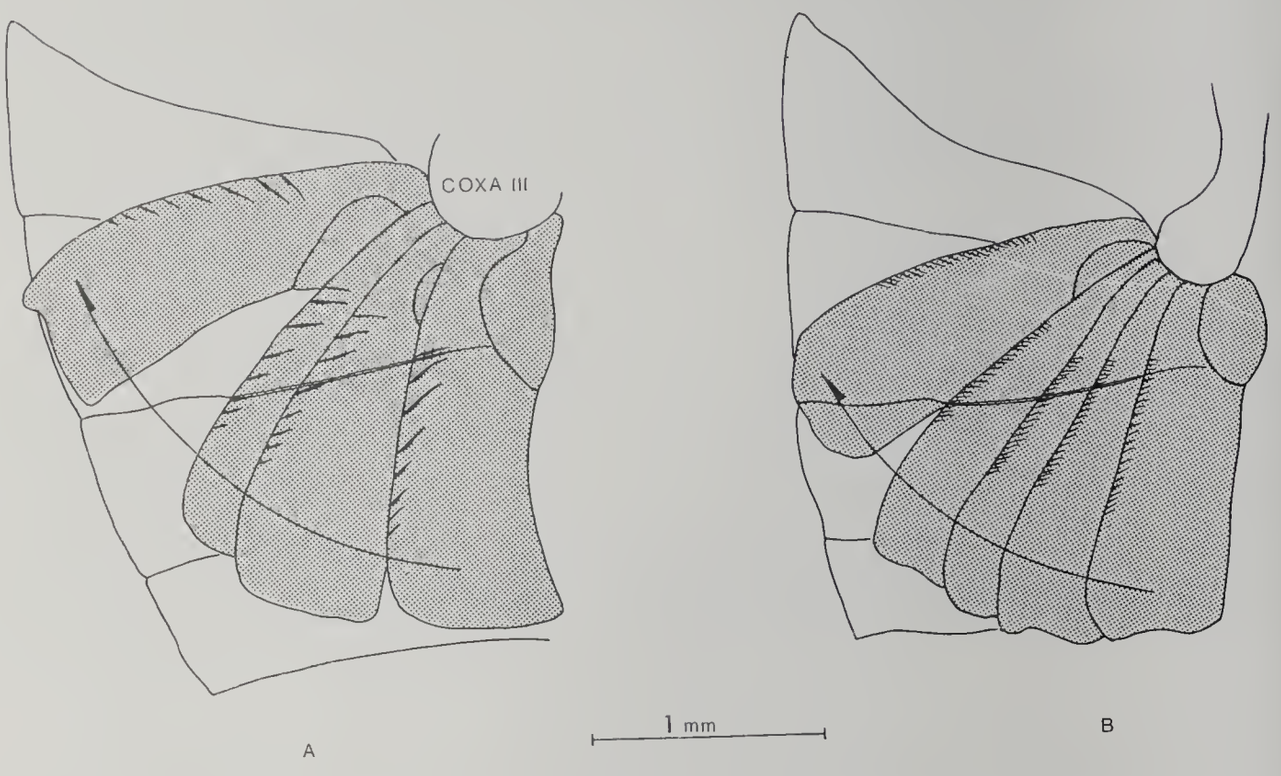

Fig. 1. Movement of metafemur over sternal plectrum in (a) *Agabus aeruginosus* and (b) *A. falli*, showing alignment of femoral grooves with the sternal plectrum.

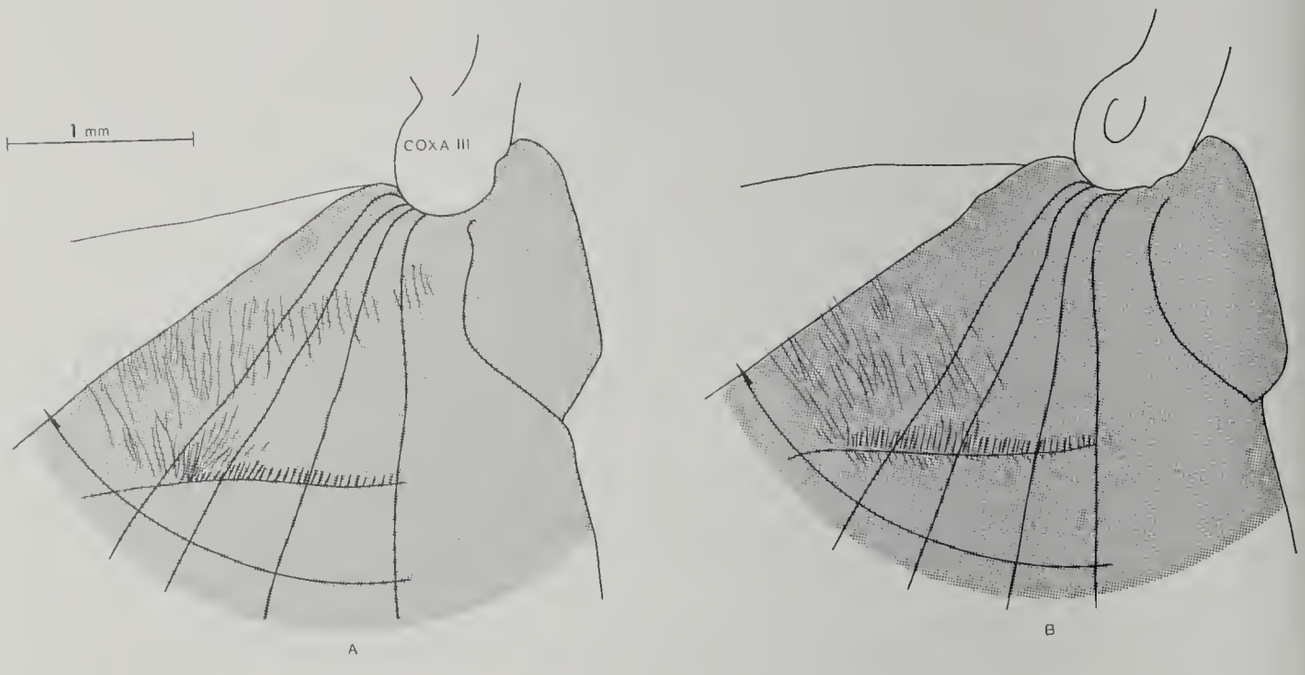

Fig. 2. Movement of metafemur over sternal file in *Colymbetes sculptilis*: (a) male; (b) female. See text for further information.

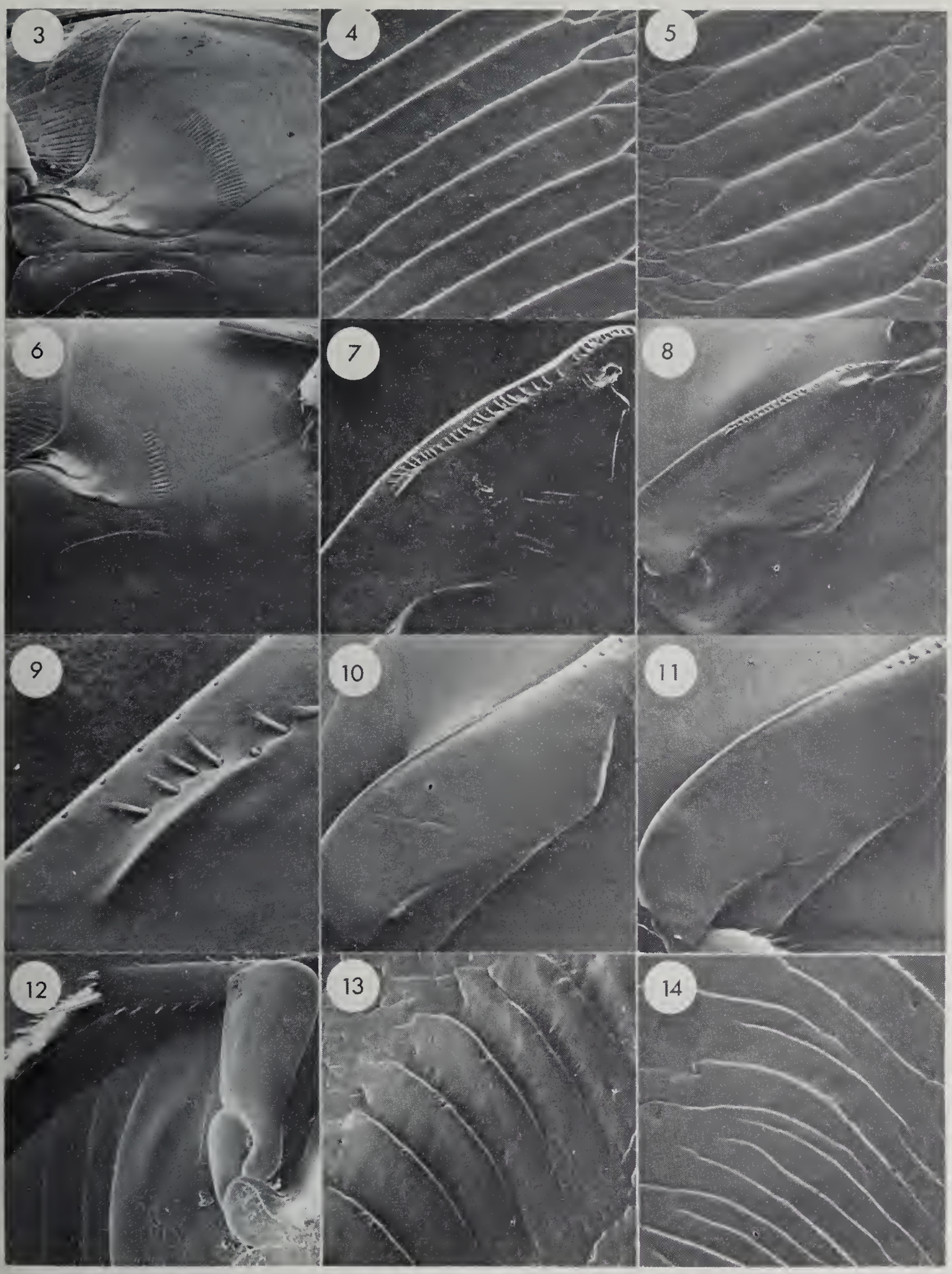

Fig. 3. *Laccophilus maculosus decipiens*: coxal file; x 22.
Fig. 4. *L. m. decipiens*: ibid; x 225.
Fig. 5. *L. fasciatus*: ibid; x 225.
Fig. 6. *L. fasciatus*: ibid; x 22.
Fig. 7. *L. maculosus decipiens*: dorsal view of metafemur showing femoral plectrum; x 40.
Fig. 8. *L. fasciatus*: ibid; x 40.
Fig. 9. *L. maculosus decipiens*: ibid; x 187.
Fig. 10. *Agabus semipunctatus*: dorsal surface of metafemur with anterior ridge; x 37.
Fig. 11. *A. velox*: ibid; x 37.
Fig. 12. *A. semipunctatus*: file of abdominal sternum 2; x 20.
Fig. 13. *A. semipunctatus*: ibid; x 187.
Fig. 14. *A. velox*: ibid; x 187.

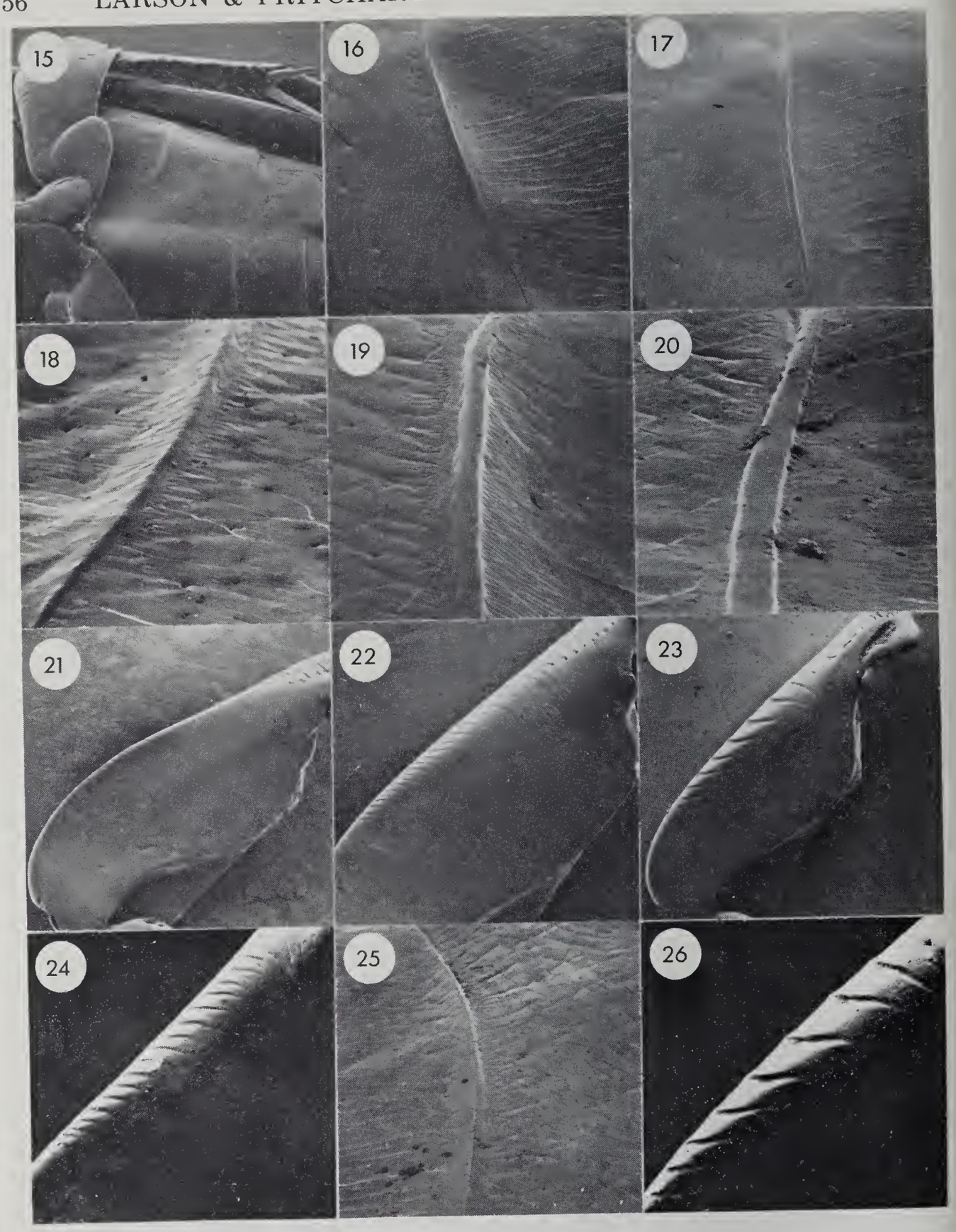

Fig. 15. *A. pisobius*: plectrum on suture between abdominal sterna 2 and 3; x 20.
Fig. 16. *A. punctatus*: ibid; x 37.
Fig. 17. *A. aeruginosus*: ibid; x 37.
Fig. 18. *A. pisobius*: ibid; x 205.
Fig. 19. *A. punctatus*: ibid; x 180.
Fig. 20. *A. aeruginosus*: ibid; x 200.
Fig. 21. *A. pisobius*: dorsal view of metafemur with anterior file; x 37.
Fig. 22. *A. punctatus*: ibid; x 37.
Fig. 23. *A. aeruginosus*: ibid; x 27.
Fig. 24. *A. falli*: ibid; x 55.
Fig. 25. *A. disintegratus*: plectrum on suture between abdominal sterna 2 and 3; x 75.
Fig. 26. *A. aeruginosus*: dorsal view of metafemur; x 55.

Genus *Loccophilus* Leach

Zimmerman (1970) recorded 27 North American species of this genus, and 12 possess a file on each metacoxal plate. Certain Palaearctic species also bear similar organs. There is intraspecific variation in the number and coarseness of lines in the file. The file is absent or less developed on females.

1. *Laccophilus maculosus decipiens* LeConte. The organ is present on the male only. The file (Fig. 3,4) consists of 35 to 45 lines (Zimmerman 1970), each about 140μ long. A well developed ridge of about 140μ long is present anteriomedially on the dorsal surface of the metafemur (Fig. 7,9). The ridge is positioned so that it passes directly over the file as the leg swings in an arc across the metacoxa.

2. *Laccophilus fasciatus* Aubé. The coxal file (Fig. 5,6), present on the male only, consists of 20 to 30 lines (Zimmerman 1970), each about 100μ long. Compared with *L. maculosus*, the entire file is located closer to the base of the metacoxa and the lines are shorter, broader, and deeper. The dorsal face of the metafemur possesses a short ridge (Fig. 8) of about the same length as the width of the file.

Genus *Hydrovatus* Motschulsky

Young (1963) noted a ridge bearing cross-striations on the anterior border of the meta-coxa of 2 Palaearctic species, *H. cuspidatus* Kunze and *H. clypealis* Sharp. A similar structure has not been found on any New World species, although we have not examined specimens of *Hydrovatus*. Young suggested that the structure forms part of a stridulatory organ but did not give a description of how the organ might operate.

Genus *Agabus* Leach

Organs of the file-and-ridge type occur on only a few species of this large genus. Two types of organ have been observed: 1) the file occurs on the mediolateral portion of visible abdominal sternum 3, and a ridge is present on the anterior margin of the metafemur; 2) a ridge occurs along the mediolateral portions of the suture between visible abdominal sterna 2 and 3, and the anterior margin of the metafemur is cross-striated to produce a file. Interspecific differences in these structures involve the width and sharpness of the ridge and the coarseness of the file.

1. *Agabus semipunctatus* Kirby. The male possesses a very strongly developed file on the mediolateral area of visible abdominal sternum 3 (Fig. 12, 13). The lines are deep and the intervening ridges slope gradually posteriorly and internally, but abruptly externally and anteriorly. The anterior dorsal margin of the metafemur is delimited by a longitudinal submarginal groove (Fig. 10). The file is arranged in a more or less concentric arc around the base of the leg. A similar organ occurs on the Palaearctic species *affinis* Paykull and *unguicularis* Thoms. (Guignot 1933).

2. *Agabus velox* Leech. This species is closely related to *A. semipunctatus* Kirby, and the males possess an organ of basically the same type. However, the sternal file (Fig. 14) is more irregular without the lines so strongly raised or showing a definite orientation. Also, the groove on the metafemur (Fig. 11) is not so well defined.

3. *Agabus falli* A. Zimmerman. Although this species is apparently closely related to *A. semipunctatus* Kirby, the file-and-ridge organ consists of the reverse type; that is the file (Fig. 24) occurs on the anterior dorsal surface of the metafemur and the ridge is formed from the elevation of the suture between visible abdominal sterna 2 and 3. Only the male possesses such an organ. The file is moderately coarse and more or less unspecialized in that the lines run rougly at right angles to the leading edge of the femur (Fig. 1b), and parallel to each other throughout much of the length of the organ.

4. *Agabus pisobius* Leech. The organ, which consists of a sharp abdominal ridge (Fig. 15, 18) and a fine femoral file (Fig. 21), is equally developed on both sexes.

5. *Agabus punctatus* Melsheimer. The organ is found on the male only. The sternal ridge (Fig. 16, 19) is fairly broad and somewhat rounded medially. The femoral file (Fig. 22) is about as coarse as that of *A. falli*. However, there is a greater tendency for the lines on the distal half of the femur to run obliquely in from the margin rather than be oriented at right angles to the margin.

6. *Agabus aeruginosus* Aubé. The organ possessed by the male is similar to that of *A. punctatus*, to which *A. aeruginosus* is closely related. The ridge (Fig. 17, 20) is broad with a low profile, and the file (Fig. 23, 26) is extremely coarse. The lines of the file are almost at right angles to the leading margin of the femur basally, but become oblique distally so that as the leg swings forward over the ridge, the lines maintain their longitudinal axis at right angles to the longitudinal axis of the ridge (Fig. 1a).

7. *Agabus disintegratus* Crotch. The sternal ridge (Fig. 25) is sharp and curved so that its anterior face is concave, and the femoral file (Fig. 27, 28) is extremely fine, formed from numerous short transverse lines. This development occurs only in the male. *Agabus taeniolatus* Harris, a closely related species, possesses a similar organ on the male (Fig. 29).

Genus *Carrhydrus* Fall

Carrhydrus crassipes Fall, the only species of this endemic North American genus, possesses a peculiar organ formed by the labial palpi and the submentum (Fig. 30, 31). The penultimate article of each palpus is triangular in shape, with a sharp ventral and 2 lateral ridges. The anterior margin of the submentum is raised laterally and bears a series of coarse longitudinal ridges. When the palpus is bent backwards and swung laterally, the median portion of the ventral ridge passes over the striae on the submentum. These structures are present and equally developed on both sexes. Fall (1922) described the peculiar structure of the labial palpus but did not suggest a function for it.

Genus *Colymbetes* Clairville

The relevant structures in this genus consist of a sternal file and a ridge on the anteror margin of the metafemur. The file occurs on the mediolateral portion of the hind margin of visible sternum 2 (Fig. 32, 33, 34, 35). The area comprising the file is slightly raised and coarsely longitudinally striate. On most specimens, the striae are longitudinally arranged medially, but become oblique laterally in a manner which maintains their longitudinal axis at right angles to the arc transversed by the femur (Fig. 2a). The file is present on both sexes of all species that we examined. However, on females of at least *C. sculptilis* Harris, the file is not so strongly raised as on the male. In addition, the striae on the female are slightly shorter and weaker, and the orientation of the ridges is roughly longitudinal throughout the length of the file and does not shift to a more oblique position laterally in correlation with the changing angle of incidence of the femur (Fig. 2b). Between species, the file varies in coarseness and in number of ridges from the few large coarse ridges of *C. fuscus* L. to the more numerous fine ridges of *C. sculptilis*. A ridge is formed by the sharp anterior margin of the metafemur which is limited dorsally by a shallow submarginal longitudinal groove similar to that shown by *Agabus semipunctatus*.

These structures were known to Gahan (1900) who queried the stridulatory function assigned to the system by previous authors, on the basis that specimens of *Colymbetes* had not been heard to stridulate. Balfour-Browne (1950) illustrated the sternal file of the species *fuscus* L. and *striatus* L.

Genus *Cybister* Curtis

Crotch (1873) first described the organ possessed by this genus. The organ, present only on males, consists of a series of short coarse grooves on the inner basal margin of the metacoxa (Fig. 36) and a corresponding ridge on the dorsal basal surface of the metatibia (Fig. 37). The number of grooves in the file varies between species. The file and ridge of *C. fimbriolatus* Say are illustrated in this paper.

Genus *Hydaticus* Leach

An unusual organ is present on the front legs of the males (Fig. 38, 39) of all North American species, and at least several Palaearctic species. The coarsely pitted dorsal surface of the second tarsal article (Fig. 31, 42) could act as a file across which can be moved a row of stout spines situated on the external margin of the protibia (Fig. 40). During the forward motion of the tibia, the movable spines bend backwards and upwards; however, during the backstroke, the spines are held perpendicularly by a ridge which passes across the anterior basal margin of the spine row. Although the pitted sculpture of the protarsus has been described for some European species (Rye 1859, *in* Balfour-Browne 1950), a function has not been postulated for it.

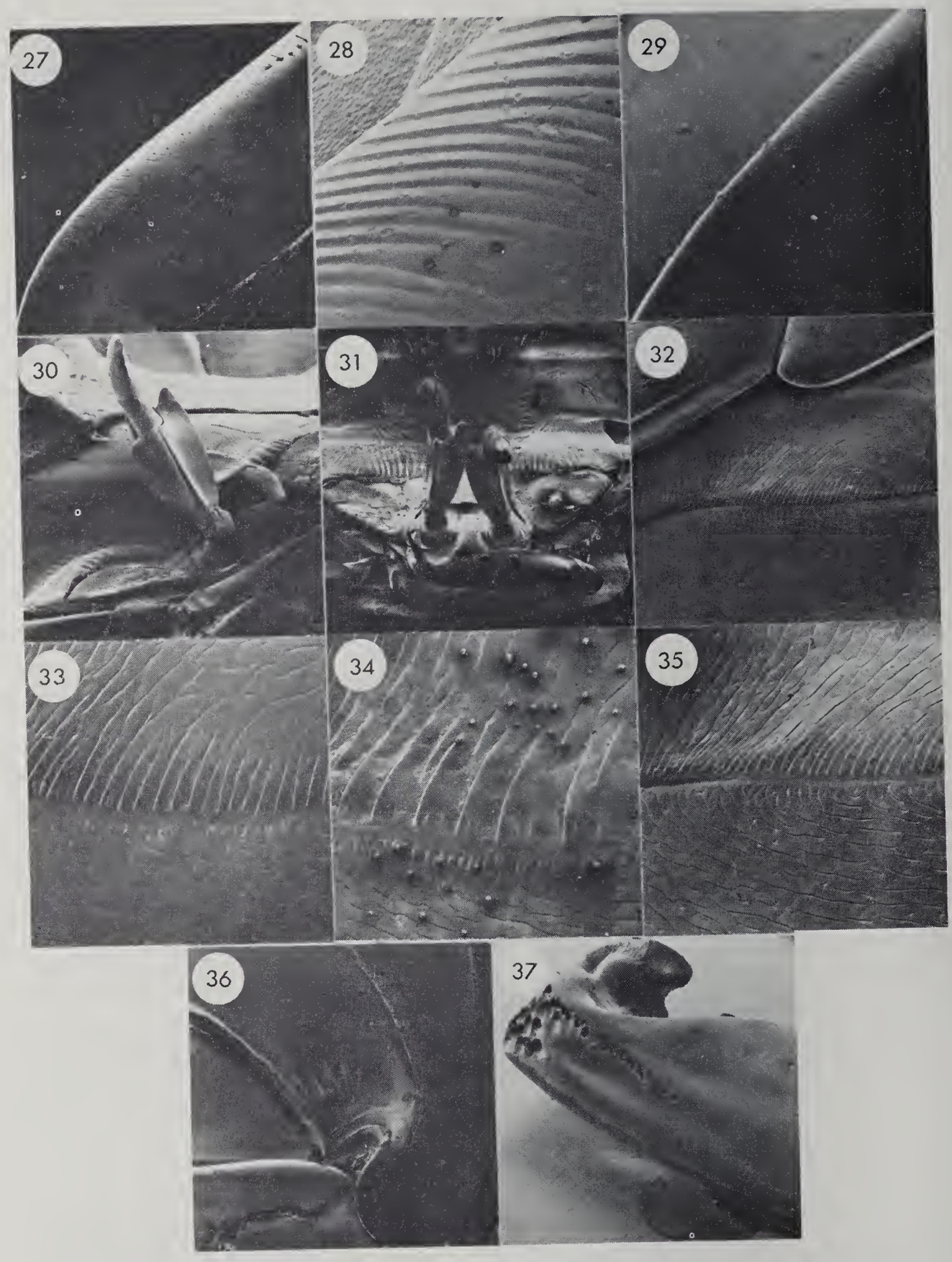

Fig. 27. *A. disintegratus*: ibid; x 37.
Fig. 28. *A. disintegratus*: ibid; x 375.
Fig. 29. *A. taeniolatus*: ibid; x 55.
Fig. 30. *Carrhydrus crassipes*: ventral surface of head, lateral view of labial palpus and submentum; x 26.
Fig. 31. *C. crassipes*: ventral surface of head, anterior view; x 23.
Fig. 32. *Colymbetes sculptilis*: file of abdominal sternum 2; x 20.
Fig. 33. *C. exaratus*: ibid; x 42.
Fig. 34. *C. fuscus*: ibid; x 42.
Fig. 35. *C. sculptilis*: ibid; x 42.
Fig. 36. *Cybister fimbriolatus*: metacoxal file; x 9.
Fig. 37. *C. fimbriolatus*: base of metafemur, dorsal view; x 220.

Discussion

The structures described here possess the morphological requirements of stridulatory organs of the type termed "frictional mechanisms" by Haskell (1961). Some, such as those of *Laccophilus maculosus decipiens* or *Agabus disintegratus* possess a file of a fineness comparable with acknowledged sound-producing mechanisms in other groups such as the Orthoptera. Others, which are clearly of the same morphological type as the above (e.g., *Cybister* or *Agabus aeruginosus*), are much coarser but nevertheless compare with published drawings of certain frictional stridulatory organs in both Orthoptera and Hemiptera (Haskell 1961). Also, in those organs with a coarse sculpture, the orientation between the ridge and the lines on the file, as the parts move across each other, is much more precisely matched than in species with fine sculpture (Fig. 1).

With the exceptions of *Agabus pisobius*, all species of *Colymbetes* examined, and *Carrhydrus crassipes*, well-developed structures of this type are present on the males only. They probably function primarily in courtship.

The described structures fall into 5 groups, based on the position on the body: 1). File on submentum, ridge on labial palpus (*Carrhydrus*). 2). File on coxa, ridge on metafemur (*Laccophilus, Hydrovatus, Cy-*

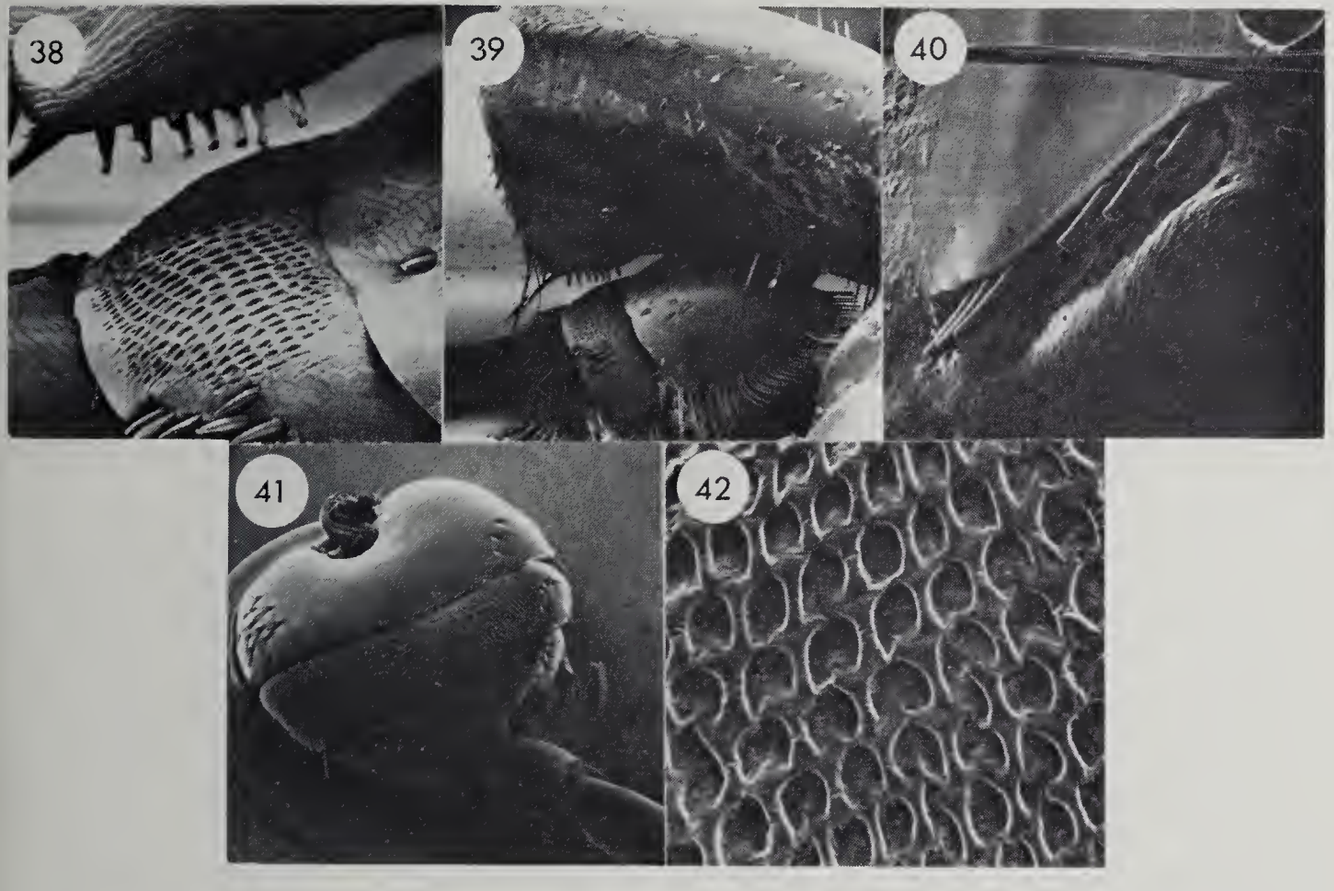

Fig. 38. *Hydaticus modestus*: left front leg, posterior view of protibial spines and tarsal articles 1 to 3; x 75.
Fig. 39. *Hydaticus modestus*: ibid; x 20.
Fig. 40. *Hydaticus modestus*: protibial spines; x 110.
Fig. 41. *Hydaticus modestus*: left protarsus, dorsal view; x 20.
Fig. 42. *Hydaticus modestus*: protarsal article 2, dorsal view; x 200.

bister). 3). File on abdomen, ridge on metafemur (some *Agabus*, *Colymbetes*). 4. Ridge on abdomen, file on metafemur (some *Agabus*). 5). File on protarsal article 2, spines on protibia (*Hydaticus*).

Some of these groups are undoubtedly natural, with the stridulatory structures homologous in the species included in the group. For example, the organ possessed by the species of *Hydaticus* is very similar throughout the genus, probably having a common origin. On the other hand, taxonomically distant species have developed similar forms of organs. Certain species of the genera *Laccophilus* and *Cybister* possess a coxal file and a corresponding femoral ridge, although differences in the position and structure of these organs tend to confirm that the 2 genera are not closely related. Similarly the presence of a sternal file and femoral ridge on a few species of *Agabus* and on the species of *Colymbetes* seems to be attributable to convergence.

Only a few species of *Agabus*, all of which appear to be closely related, possess sternal files; have a different form of organ but still use essentially the same body parts. Among the North American species, the sternal ridge femoral file type of organ is found in 4 groups: 1) *falli* group; 2) *punctatus - aeruginosus* group; 3) *disintegratus* group; 4) *pisobius* group. While these species represent a single section of the large genus *Agabus*, it is doubtful that these organs were all inherited from a single ancestral stock; *A. pisobius* is very similar to *A. punctulatus* Aubé, *oblongulus* Fall, and *colymbus* Leech, but none of the latter possess possible stridulatory organs. While the latter 3 species are allopatric, the range of *pisobius* overlaps the distribution of both *punctulatus* and *oblongulus* and a stridulatory organ could provide an isolating mechanism. Two of the 3 species of the *disintegratus* group, namely *A. disintegratus* Crotch and *A. taeniolatus* Harris, possess possible stridulatory organs, while the third species, *A. lineellus* LeConte, lacks an organ. Both species of the *punctatus* group, *punctatus* Melsheimer and *aeruginosus* Aubé, have metafemoral files and sternal ridges. *Agabus falli* appears to be closely related to *A. semipunctatus* on the basis of habitus and male sexual and secondary sexual characters, yet it has an organ of a different type.

If the function of these organs is sound production then these observations support the views of Alexander, Moore, & Woodruff (1963): "The rudimentary nature of acoustical behavior in beetles—coupled with the great number and variety of species and systems involved—makes this kind of behavior in these particular animals an appropriate subject for the study of evolutionary direction in the early elaboration of communicative systems."

Acknowledgments

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